Sex differences in Little Auk *Alle alle* parental care: transition from biparental to paternal-only care

ANN M. A. HARDING,[1*] THOMAS I. VAN PELT,[1,2] JAN T. LIFJELD[3] & FRIDTJOF MEHLUM[3]
[1]*Polish Polar Station in Hornsund, Institute of Geophysics, Polish Academy of Sciences, Spitsbergen, Norway*
[2]*Alaska Science Center, US Geological Survey, 1011 E. Tudor Road, Anchorage, AK 99503, USA*
[3]*Zoological Museum, Natural History Museums and Botanical Garden, University of Oslo, PO Box 1172, Blindern, N-0318 Oslo, Norway*

Understanding differences in male and female care in biparental care systems can help interpret the selective pressures that shape parental strategies. We examined Little Auk *Alle alle* parental care at a breeding colony during the chick-rearing and fledging periods by conducting observations on marked, known-sex pairs, and by examining the sex ratio of birds carrying food to the colony. Little Auks transitioned from biparental to mostly paternal-only care during late chick-rearing. Males delivered more meals and spent more time at the colony than females during late chick-rearing. Very few females were present at the colony by the end of chick-rearing and through the fledging period, and all marked parents observed accompanying their chick to sea were male. Chick mass loss prior to fledging was associated with the lack of provisioning by the female parent, rather than a reduction in feeding frequency by both parents. The occurrence of paternal-only care during and after fledging is discussed in relation to physiological, ecological and phylogenetic constraints.

Parental care describes any parental behaviour that is likely to increase the fitness of offspring (Clutton-Brock & Godfray 1991). Many studies of biparental care systems have examined parental roles, the relative extent of male and female care, and the selective pressures driving these differences (e.g. Clutton-Brock 1991, Gowaty 1996, Szëkely & Cuthill 2000). Differences in parental care may reflect a variety of constraints imposed by physiological, ecological and behavioural factors, including: sex differences in the costs of parental investment, such as egg production (Monaghan *et al.* 1998); confidence of paternity (Davies *et al.* 1992); sexual size dimorphism (Owens & Hartley 1998); energy requirements of the young (Carere & Alleva 1998); and food supply (Uttley 1992). Quantification of differences in male–female care within species helps to understand the evolution of parental strategies, and an understanding of male–female differences among closely related species that share biparental breeding systems can provide further insights into the selective pressures and phylogenetic constraints that shape patterns of parental care.

Seabirds are noted among avian species for their small clutch sizes, long developmental periods, prolonged parental care and low annual reproductive output (Charlesworth 1980, Ricklefs 1990). These traits are thought to reflect the sparse, patchy and unpredictable distribution of marine food resources (Lack 1968). All seabird species have biparental care, and for many species, biparental care is essential for reproductive success (Gowaty 1996). Although both sexes may invest more or less equally in parental care, males and females often differ in their specific parental roles (e.g. Creelman & Storey 1991, Bradley *et al.* 2002), foraging behaviour (Weimerskirch *et al.* 1997, Gray & Hamer 2001a) or the timing of certain forms of parental care across the incubation and chick-rearing period (e.g. Ainley *et al.* 2002).

The Alcidae is a diverse family of seabirds, exhibiting high variation in adult body size, nesting habitat, degree of coloniality, social behaviour and feeding ecology among the 22 extant species (Gaston & Jones 1998). The Alcidae is also characterized by marked interspecific variation in chick development and fledging strategies, male–female parental care, and the

*Corresponding author. Present address: Alaska Science Center, US Geological Survey, 1011 E. Tudor Road, Anchorage, AK 99503, USA.
Email: ann_harding@usgs.gov

allocation of parental care during the pre-fledging (at the colony) and post-fledging (at sea) breeding phases (Sealy 1973, Gaston 1985, Ydenberg 1989). Examination of parental care within the Alcidae, in the context of species-specific physiological, ecological and phylogenetic constraints, may help to interpret the selective pressures driving sex differences in care in biparental systems. Such interpretation requires an understanding of parental care across the range exhibited among the Alcidae, yet the role of males and females in parental care remains incompletely understood for some alcid species.

The Little Auk *Alle alle* is an important example among the Alcidae. Little Auks belong to the tribe Alcini, together with the Brünnich's Guillemot *Uria lomvia*, the Common Guillemot *Uria aalge* and the Razorbill *Alca torda* (Strauch 1985). Both Guillemot species and the Razorbill have a chick developmental pattern termed an 'intermediate' strategy by Sealy (1973), whereby chicks have biparental care at the nest-site until they leave the colony at 15–30% of adult body weight, at 15–30 days old (reviewed in Gaston 1985), and are led out to sea by the male parent. Paternal-only care continues at sea for at least 1–2 months (Harris & Birkhead 1985, Gaston & Jones 1998, Ainley *et al.* 2002), with the parent feeding and guarding the chick, and leading it to good foraging areas (Sealy 1973). Little Auk chicks are also accompanied to the sea by one parent (Stempniewicz 1995), and there is some evidence of post-fledging parental care. However, Little Auk chicks leave the colony older, more developed and at a higher percentage of adult body mass than the other members of the tribe, fledging between 67 and 82% of adult body mass, at an average age of 27 days (Norderhaug 1980, Stempniewicz 2001). The occurrence of parental care during and after colony departure in the Little Auk is unusual among the Alcidae, because chicks from all other species that leave the nest-site at a similar percentage adult body mass are independent during and after leaving the colony.

Previous studies have shown a male bias in captured Little Auk adults carrying chick meals during late chick-rearing (Roby *et al.* 1981, Taylor 1994, Stempniewicz 1995), and Little Auk adults that have been collected while accompanying their fledged chick at sea have been male (Bradstreet 1982). However, because there have been no observations on sexed birds, sex differences in provisioning have only been inferred, there have been no observations on known-sex parents leaving the colony with the chick, and the non-provisioning aspects of parental care remain largely unknown.

Using molecular sexing of captured adults, we quantified sex differences in Little Auk parental care at a breeding colony during the chick-rearing and fledging periods by (a) conducting observations on marked, known-sex pairs, and (b) examining the number of males and females caught carrying food to the colony. We present data on sex differences in provisioning, foraging-trip durations and time spent at the colony and in the nest, and discuss results in relation to ecological, physiological and phylogenetic constraints.

METHODS

Little Auks are planktivorous and socially monogamous, have very slight sexual size dimorphism, and rear a single chick annually. Little Auks breed in the Arctic, nesting in enclosed rock crevices in talus or boulder scree slopes, and colonies can be on the coast or on mountain slopes up to 30 km inland (Gaston & Jones 1998).

We studied Little Auks at a large colony located on the southern slopes of Ariekammen (Mount Arie), on the northern shore of Hornsund Fjord, Spitsbergen (77°00′N, 15°22′E). Little Auks nest in rock crevices on the talus slopes of Ariekammen, and their breeding biology has been described previously by Norderhaug (1980) and Stempniewicz (1980, 1981). Fieldwork was conducted between 7 July and 24 August 2002.

Twenty-four accessible nests were found towards the end of the incubation period (8–11 July). All 24 nests were followed for hatching chronology and fledging age, but only 15 of these nests had single visible nest entrances and were used for observations. Nests were checked every 1–3 days until hatching, and daily during the fledging period. Because initial data on the age of chicks was unknown within the range 0.5–1.5 days old, we standardized chick age as age 1 day on the date when first detected. During each visit the nest chamber was checked either by using a headlamp or by feel (depending on chamber depth), and the presence of adult, chick or egg was recorded.

Parental provisioning and time spent at the colony

Both parents from 14 of the 15 visible nests were captured at the nest-site while incubating, and identified with an individual colour ring combination and with marker pen on the breast feathers. Each adult

was assigned an identification number, with nest number plus either an A or B. Only one parent was captured at one of the 15 nests, and this bird is excluded from paired comparisons.

A small blood sample (25 μL) was taken from the brachial vein of each adult for later sex identification. The blood sample was immediately suspended in 1 mL lysis buffer (Seutin *et al.* 1991) and stored at 4 °C for 2–3 months until analysed in the DNA laboratory at the Zoological Museum, Oslo. DNA was extracted in the laboratory from 200 μL blood solution, using the QIAamp Mini Kit (QIAGene). Molecular sexing was performed with the primer pair 2550F and 2718R according to the protocol described by Fridolfsson and Ellegren (1999). These primers amplify a 400–450-bp fragment on the W chromosome (i.e. in females only), and a 600–650-bp fragment on the Z chromosome (both sexes). This size difference is clearly visible when separating the fragments on an agarose gel.

Twenty-four-hour watches were conducted during early, mid and late chick-rearing to quantify sex differences in parental behaviour across the chick-rearing period. We assume that each 24-h watch is representative of each chick-rearing phase (early, mid and late). Owing to the wide dispersion of nest-sites that have both viewable entrances and accessible nest chambers, we split the 15 nests into two groups, allowing two people to observe all nests simultaneously. Two observers conducted a 24-h watch on 19 July (early chick-rearing phase; mean chick age = 3.8 days). Three observers conducted the remaining two 24-h watches on 31 July (mid chick-rearing phase; mean chick age = 15.6 days) and 8 August (late chick-rearing phase; mean chick age = 21.4 days). Nest visibility constraints during the first watch and breeding failure reduced the total number of nests observed to 13 (including the one single bird) for early chick-rearing, and 14 (including the one single) for mid and late chick-rearing. We recorded the following data during each watch: (1) Time of marked bird's arrival and departure at the study site. These observations were used to calculate total time spent at the colony (min) and forage trip duration (min). (2) Time of entry and exit from the nest site. (3) Food delivery. Birds bring zooplankton to their chick in a gular pouch (Stempniewicz 2001), and provisioning parents are easily recognized by their bulging throat. (4) The occurrence of stereotypical aggressive interactions such as lunging, pecking, biting and grasping (described in Jones *et al.* 2002b). Because only two observers conducted the early chick-rearing

watch, priority was placed on food deliveries, and foraging trip durations and time at the colony were only recorded from a smaller subset (*n* = 8) of the nests.

Sex ratio of adults carrying food

We examined the number of males and females carrying food, presumably for the chick, to provide additional data on sex roles during the provisioning period. Birds carrying food were caught during both the middle (*n* = 20, 2–5 August) and the late (*n* = 42, 10–12 August) chick-rearing periods. Birds were captured from subcolonies separate from the observation birds, and no colour-ringed individuals were caught during these capture sessions.

Birds were caught either by long-handled hand net or by mist-net. The hand net was used to catch individuals standing on rocks in the colony, whereas the mist-net caught birds in flight either departing or arriving at the colony. A small amount of blood (25 μL) was taken from the brachial vein from each adult caught with food for later sex identification, and the birds were released without harm *c.* 5 min after capture. Captures were distributed across all hours to avoid potential diurnal differences in provisioning.

Chick mass recession

In order to determine the timing of peak mass and mass recession, accessible chicks (*n* = 11 chicks) were weighed every 2–4 days from 30 July until fledging, using a Pesola balance with precision of ± 1.0 g.

Fledging watches

Little Auk chick departure from the colony has generally been termed 'fledging' (Stempniewicz 2001). For clarity, here we also use 'fledging' to refer to Little Auk colony departure, although we recognize that chicks may not be fully independent at that stage.

In addition to the three 24-h watches, we conducted four fledging watches (9–12 August) during the peak fledging period (22:00–02:00 h) to quantify male–female parental behaviour associated with fledging (*n* nests observed per watch = 9, 9, 4, 2, respectively). Most birds (83%, total *n* = 11 nests) were observed during their fledging night even if the fledging event occurred after the watch had ended, and all nests observed were within 2 days of their chick's eventual fledging date. The same behavioural parameters as described above were recorded for the duration of each fledging watch.

Ethical note

All birds were handled under permission of the Norwegian Animal Research Authority. Handling times of chicks and adults were minimized to 5–10 min, and care was taken to keep the birds comfortable while being handled.

RESULTS

Chick feeding

In total, 211 meal deliveries were observed over the three observation phases. The mean total number of chick meals delivered per chick differed among observation phases (one-way ANOVA: $F_{2,35} = 4.25$, $P = 0.022$: early mean = 4.8 meals per chick (se = ± 1.0); mid mean = 7.7 (se = ± 0.9); late mean = 4.1 (se = ± 0.9)), with chicks being fed significantly more meals during mid chick-rearing than during late chick-rearing (Tukey multiple comparison test: $P < 0.05$).

There was no significant difference in the number of meals delivered by males and females during either the early (paired t-test: $t_{11} = 0.4$, $P = 0.70$) or the mid chick-rearing phase (paired t-test: $t_{12} = 1.92$, $P = 0.08$), although there was a trend towards males delivering more during mid chick-rearing. Males delivered significantly more meal loads than females during late chick-rearing (Wilcoxon paired-sample test: $W = 66$, $n = 13$, $P = 0.004$; Fig. 1). Only three of the 13 females watched on 8 August brought food to the colony, and two of those birds did not actually deliver any food to their chick.

There was no significant difference in the mean number of meals delivered by males among the three observation phases (one-way ANOVA: $F_{2,35} = 1.99$, $P = 0.32$), or by females between early and mid chick-rearing (two-sample t-test: $t_{16} = 0.9$, $P = 0.38$).
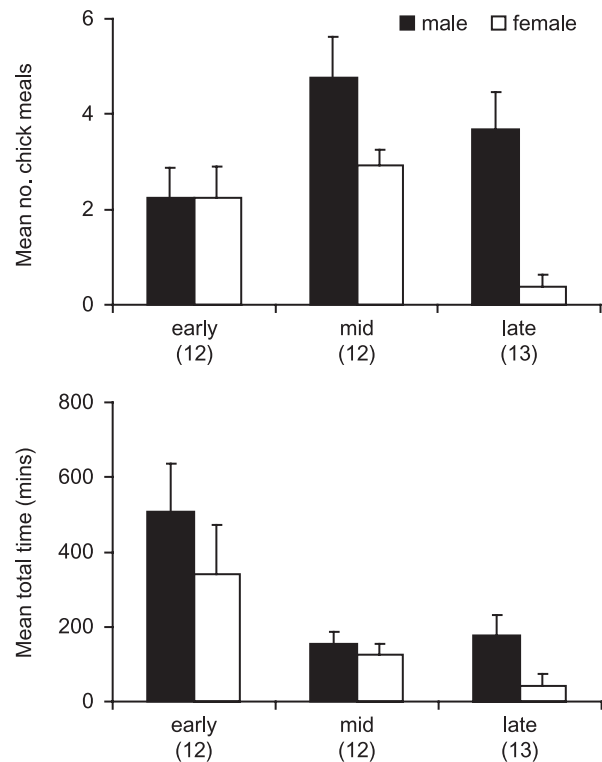

Figure 1. Top: sex differences in provisioning of known-sex breeding pairs of Little Auks. Mean (± 1 se) number of chick meals delivered by males and females per 24 h are presented. Bottom: sex differences in mean total time spent at the colony (total min ± 1 se) per 24 h. Numbers of pairs observed are given in parentheses for both graphs.

Forage trip durations

There was a wide range in duration of Little Auk foraging trips (Table 1). Considering foraging trips from all three chick-rearing watches, mean trip duration was 158 min ($n = 156$, sd = ± 140, range = 22–767 min).

The mean trip duration (both male and female) did not differ among the three phases of chick-rearing (one-way ANOVA: $F_{2,48} = 0.33$, $P = 0.72$). The duration

Table 1. Foraging trip durations (min) of male and female Little Auks during the three phases of chick-rearing. n = number of individuals observed that delivered chick meals. Means presented are means of mean trip duration per individual.

Phase	Male				Female				Total			
	Mean	n	sd	Range	Mean	n	sd	Range	Mean	n	sd	Range
Early	153.0	7	62.2	31–202	146.7	6	85.3	41–264	150.2	13	70.6	31–264
Mid	189.5	12	159.3	69–590	145.3	13	141.5	54–591	166.7	25	148.8	54–591
Late	155.9	11	88.5	74–323	374.5	2	48.8	340–409	189.5	13	116.0	74–409

of foraging trips made by males also did not differ among the three phases of chick-rearing (one-way ANOVA: $F_{2,27} = 0.31$, $P = 0.74$). As foraging trip durations were only recorded on a subset of birds (eight nests) during early chick-rearing, and not all individuals observed delivered meals, there were too few data to examine female trip duration across chick-rearing.

There was no significant difference between male and female forage trip durations during middle chick-rearing (two-sample *t*-test: $t_{22} = 0.73$, $P = 0.48$). There were too few data to examine sex differences in trip durations during early and late chick-rearing.

Time at the colony

The mean time spent at the colony by both parents differed among observation phases (Kruskal–Wallis test: $H_2 = 13.09$, $P = 0.001$), with birds spending significantly more time at the colony during early chick-rearing than during either mid or late chick-rearing (Nemenyi test, $P < 0.05$; Fig. 1).

There were also sex differences in the time budgets of males and females (Fig. 1). Male time at the colony differed among observation phases (Kruskal–Wallis test: $H_2 = 6.45$, $P = 0.04$). Males spent significantly longer at the colony during early chick-rearing than during either mid or late chick-rearing (Nemenyi test: $P < 0.05$). Female time at the colony also differed among observation phases (Kruskal–Wallis test: $H_2 = 11.36$, $P = 0.003$), with females spending significantly less time at the colony during late chick-rearing than during either early or mid chick-rearing (Nemenyi test: $P < 0.05$).

The parents differed in their time spent at the colony within observation phases (Fig. 1). Although there was no difference in the time that they spent at the colony during either early (Wilcoxon paired-sample test: $W = 21$, $n = 7$, $P = 0.27$) or mid chick-rearing (Wilcoxon paired-sample test: $W = 58$, $n = 13$, $P = 0.40$), males spent significantly longer at the colony than females during late chick-rearing (Wilcoxon paired-sample test: $W = 79$, $n = 13$, $P = 0.02$).

Time spent in the nest

Birds spent more time in the nest during early chick-rearing than during mid and late chick-rearing (Table 2). There were no sex differences in time spent in the nest during either early (Wilcoxon paired-sample test: $W = 21$, $n = 7$, $P = 0.27$) or mid chick-rearing ($W = 58$, $n = 13$, $P = 0.40$). Because of sharply reduced female provisioning, we had insufficient data to test

Table 2. Time spent in the nest by males and females during the three phases of chick-rearing. n = number of nests observed with both parents marked. Means are given in minutes, and percentage is the percentage of total time at the colony spent in the nest.

Phase	n	Males			Females		
		Mean	sd	%	Mean	sd	%
Early	9	372.6	340.6	47.8	307.3	334.2	46.6
Mid	13	8.7	9.2	6.0	9.1	7.1	8.8
Late	13	5.8	1.6	5.1	0.2	0.6	0.0

for sex differences in nest attendance at the end of chick-rearing.

Aggressive or territorial behaviour

During all three 24-h chick-rearing watches, we observed only one aggressive interaction involving a marked bird. One breeding female was blocked from delivering food to her chick by another bird (unknown status and sex). Her bill was grasped and she dropped some food before managing to enter her nest.

Sex ratio of birds caught delivering food

We found no significant sex bias in birds captured carrying food during mid chick-rearing (2–5 August; males = 12, females = 8; $\chi_1^2 = 0.8$, $P > 0.05$). Of the 39 birds caught at the end of chick-rearing (10–12 August), there were significantly more males than females (males = 33, females = 6; $\chi_1^2 = 18.69$, $P < 0.001$).

Chick mass recession

Chicks from observed nests were still gaining mass during the mid chick-rearing observation phase, and had reached peak mass by 7 August (Fig. 2; average date of peak mass = 5 August, $n = 11$, sd = ± 1.6). The average age at which chicks attained their peak mass was 19 days ($n = 11$, sd = ± 3.4, range = 16–25 days). Mean peak mass was 128 g ($n = 11$ chicks, sd = ± 9.7), and chicks lost on average 9.2% of peak body mass before fledging ($n = 11$ chicks, sd = ± 4.5, range = 2–17%).

Fledging

The median hatch date was 16 July ($n = 17$ nests). Fledging began on 6 August, and all chicks had left
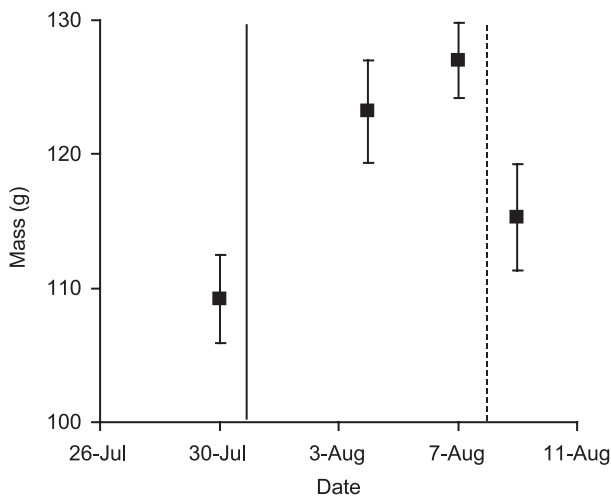
Figure 2. Mean chick mass (± 1 se) during mid and late chick-rearing observation phases (*n* = 11 chicks). Dates of 24-h watches are indicated by solid line (mid chick-rearing) and dashed line (late chick-rearing).

Table 3. Mean number of feeds and the mean time spent at the colony (min) by males and females during the fledging watches. Watch duration given in minutes. *n* = number of nests observed with both marked parents.

Date	Duration	*n*	No. of feeds		Time at colony	
			Female	Male	Female	Male
09 August	205	9	0	0.67	1	76
10 August	150	9	0	0.44	0	58
11 August	120	4	0	0.50	0	54
12 August	120	2	0	1.00	0	14

the colony by 15 August (median = 10 August, *n* = 15 chicks). The mean fledging age was 25 days (sd = ± 1.8, *n* = 15 chicks). Fourteen chicks fledged at 20–28 days, and one outlier fledged at 49 days.

Fledging watches were carried out for a total of 595 min. We made the following observations during the fledging watches (Table 3): (a) no females fed their chick during the observed periods, whereas 14 meals were delivered by males; (b) only one marked female was seen at the colony (for 10 min) during all four watches (1446 min of male attendance); (c) males from all observed pairs, with the exception of one male on 12 August, spent time at the colony during each watch period.

We observed four fledglings leaving the colony with a marked parent. Times of observed fledgings were 01:20, 01:55, 00:32 and 01:53 h. In each event,

the male parent accompanied the chick to sea and the female parent was not present at the colony. The male parent appeared to encourage the chick to move away from the nest entrance, either vocally or by running back and forth. There was much bill contact between the male parent and chick, and chicks were sometimes seen begging just prior to fledging, or giving a sharp, high-pitched fledging call very similar to those of Common Guillemot chicks departing from the colony. The chick was encouraged to the top of a nearby rock by the parent. The chick left the colony before the adult in each case, then the adult overtook almost immediately and led the chick out to sea, flying very close. No observed fledglings were fed between emergence from the nest crevice and colony departure.

DISCUSSION

We observed a strong shift through the season in the balance of parental care between parents, with no sex differences in feeding rates and time spent at the colony during early and mid chick-rearing, but with males delivering more meals and spending more time at the colony during late chick-rearing and the fledging period. Most females ceased provisioning late in the chick-rearing period and left the colony before the chick fledged; the male parent led the chick to sea.

Little Auk parental care

This is the first study to conduct observations on known-sex Little Auks and to present data on foraging-trip durations and feeding rates. We observed no sex difference in provisioning rates during early and mid chick-rearing, whereas there was a clear difference between the sexes at the end of chick-rearing, with males delivering virtually all food to their chicks.

Previous studies that have examined sex differences in Little Auk provisioning have used an indirect method (the capture and sexing of birds carrying food). The comparison between direct observations of chick feeding rates and the sex ratio of birds caught with food assumes that the sex ratio of birds carrying food at the colony is similar to the sex-specific proportion of provisioning visits to the chick. Although the capture data during mid and late chick-rearing (this study) did support the observations of feeding rates by marked birds, the sample of birds caught during mid chick-rearing was small; more observation and simultaneous capture days are

needed to qualify this comparison. Although our observations support previous studies that show a higher number of males caught with food at the end of chick-rearing (Roby *et al.* 1981, Taylor 1994, Stempniewicz 1995), studies that have examined sex differences in provisioning during early and mid chick-rearing have produced mixed results. The numbers of male and female birds caught with food during the first half of chick-rearing were equal in northeast Greenland (Roby *et al.* 1981), whereas more provisioning females than males were caught during the mid chick-rearing period in Spitsbergen (Taylor 1994).

There was no difference in forage trip duration among the early, mid and late chick-rearing observation periods, suggesting a similarity in foraging range across the chick-rearing period. Trip duration during mid chick-rearing also did not differ between males and females, and because birds leave and arrive at the colony in mixed-sex groups (A. Harding pers. obs.), it is possible that males and females forage in the same feeding areas. However, variation in trip duration is high, and the use of alternative methods (e.g. radiotelemetry) may be needed to quantify foraging locations across the chick-rearing period and between males and females.

Birds spent the most time at the colony during early chick-rearing, and a high proportion of this time was spent in the nest, presumably brooding, as chicks are brooded almost continuously until they have attained endothermy at 3–5 days (Norderhaug 1980). Males and females spent similar amounts of time at the colony and in the nest during early and mid chick-rearing, whereas females spent very little time at the colony during late chick-rearing and the fledging period.

Data on age of peak mass, peak body mass and mass at fledging recorded in this study are similar to previous studies (Norderhaug 1980, Stempniewicz 2001). Little Auk chicks undergo a period of mass recession before fledging (Stempniewicz 2001, this study), and can lose 50% of their fat mass during this period (Taylor & Konarzewski 1989). Many seabird chicks undergo a period of mass recession pre-fledging (Lack 1968). Water loss from maturing tissues may partly explain the physiology of chick mass recession (e.g. Ricklefs 1968, Taylor & Konarzewski 1989, Phillips & Hamer 1999), but in many species mass recession has been associated with a reduction in parental provisioning before fledging (e.g. Hudson 1979, Morbey *et al.* 1999, Phillips & Hamer 2000, Gray & Hamer 2001b). Mass recession and the loss

of fat reserves in Little Auks is associated with a decrease in the number of meal deliveries towards the end of chick-rearing (Stempniewicz & Jezierski 1987, this study), explained by the lack of female provisioning at this time. Little Auks are the only alcid species known to have mass recession associated with the lack of provisioning by one parent, rather than a reduction by both parents.

The mean age of chicks at fledging in this study was very similar to that reported in previous studies (27 days; Norderhaug 1980, Stempniewicz 1981), although the range in fledging age was wider than previously recorded (23–31 days; Stempniewicz 1981). The only previous evidence on the sex of Little Auk parents accompanying chicks to sea came from a study that collected adult–fledgling pairs at sea, and found the adults to be male (Bradstreet 1982). Our colony-based observations of marked male parents leading their chick to the sea, and the near absence of females at the colony during fledging (this study), confirm that it is the male parent that generally escorts the chick to sea.

Several lines of evidence suggest that Little Auk fledglings depend, at least in part, on their accompanying parent as they move out to sea: fledgling–parent couples have been observed at sea 500–600 km away from the colony (Stempniewicz 2001), and at least 10 days after the fledging period of regional colonies (L. Stempniewicz pers. obs.); diets of fledglings are very similar in both taxon and prey length to that of the parent that accompanies them (Bradstreet 1982); and chick mass continues to increase for at least 1 month after fledging (Gaston & Jones 1998). Furthermore, M.S.W. Bradstreet (pers. comm.) observed one parent feeding its fledgling at sea, and some of the adults collected accompanying their fledgling had full gular pouches. Chicks may be led to good foraging areas by their escorting parent, and Bradstreet's observations suggest that chicks may continue to be fed, at least partially, at sea by their male parent in a manner similar to the closely related guillemots (*Uria* spp.) and Razorbill.

Comparison with other species

The occurrence of parental care during and after colony departure in the Little Auk is unusual among the Alcidae. Although the Alcidae are characterized by high interspecific variation in the allocation of parental care before and after chicks leave the colony (Sealy 1973, Gaston 1985, Ydenberg 1989, 2001), chicks from all other species that leave the colony at

a similar percentage adult body mass are independent during and after colony departure. The occurrence of parental care during and after colony departure in Little Auks may be a conserved phylogenetic trait within the Alcini tribe. The Little Auk is the only species of the Alcini tribe to have been classified as having semiprecocial chick development (summarized in Sealy 1973), yet they share key elements of the parental care strategy found in the other three species of the tribe (the two *Uria* guillemots and the Razorbill) that all have intermediate chick development (see Introduction for definition). All four species share incubation duties equally between the sexes (Wanless & Harris 1986, Stempniewicz & Jezierski 1987, Verspoor *et al.* 1987), chicks from all species are accompanied to the sea by the male parent (Harris & Birkhead 1985, this study) and chicks from all four species have some post-colony departure parental care.

The sex-linked role of post-colony departure parental care in the guillemots and Razorbill has been discussed in relation to sex differences in the benefits of desertion and continued costs of parental care (Ainley *et al.* 2002). Because seabirds are long lived and have high mate fidelity across years, there is an advantage for both members of the pair to maintain their partner's condition and increase chances of survival to the following breeding season (Jones *et al.* 2002c). Females have high initial investment in egg production (Monaghan *et al.* 1998) and may be in poorer condition at the end of chick-rearing (Taylor 1994). Thus, females may benefit from deserting, where freedom from provisioning would reduce the high predation risks and flight costs associated with provisioning at the colony, and accumulating fat reserves may increase probability of breeding the following season. Out of the two sexes, males may be in better condition and consequently may risk their chances of future winter survival less than females by escorting the chick to sea, and there may also be a survival advantage for chicks to leave the colony with the slightly larger and possibly more aggressive male (Ainley *et al.* 2002).

The occurrence of paternal care after chick colony departure in the Razorbill and *Uria* guillemots has also been discussed in relation to sex differences in brooding and provisioning behaviour during chick-rearing (Wanless & Harris 1986, Jones *et al.* 2002a). However, despite the similarity of post-colony departure care by the male parent, female parental care differs between Little Auks and the other three members of the Alcini in two important ways. First, female Razorbills and *Uria* guillemots feed their chick

until colony departure, and in some colonies may even provision more than the male (Wanless & Harris 1986, Ainley *et al.* 2002). Secondly, Razorbill and guillemot females remain at the colony for several weeks after their chick and male partner have left, probably to defend their nest-site from potential competitors (Wanless & Harris 1986, Ainley *et al.* 2002).

The apparently deviating pattern of maternal care in the Little Auk may be linked to the difference in chick growth and developmental strategy between the Little Auk and the other three Alcini species. Not only do Little Auk chicks leave the colony when older, more developed and at a higher percentage of adult body mass than the other three Alcini species, but the maximum growth rate (g/day) of Little Auk chicks (expressed as a percentage of adult mass) is more than twice the rate found in the other three species (summarized in Gaston 1985). A more complete understanding of the differences in maternal care between the Little Auk and the other three species demands more information on (a) the parental effort (at the colony and at sea) associated with the two contrasting chick growth and developmental strategies in the Alcini tribe, and (b) the selective pressures shaping these different chick developmental patterns.

In addition to the influence of chick developmental pattern on parental care, the following factors might also influence the timing of female departure from the colony. (1) Nest exposure: crevice nest-sites of the Little Auk (the only truly crevice-nesting species of the tribe) provide relatively constant temperatures and protection from predators (Birkhead & Harris 1985). This allows parents to leave the chick alone and forage simultaneously, and may help explain why female Little Auks have the flexibility to leave the colony prior to chick departure. (2) Nest competition: Little Auks may face less competition for nest-sites than Razorbills and guillemots (because crevice nest-sites may be less limited in number or quality), and the benefits of remaining at the colony post-chick departure may therefore be relatively low. (3) Adult body size: adult Little Auks are substantially smaller than the Razorbill and guillemots (summarized in Birkhead & Harris 1985), and face higher risks of predation by gulls at the colony. High predation risk may increase costs associated with time spent at the colony, and may help explain why females do not remain at the colony after chick departure. Little Auk parental behaviour and chick development are unlikely to be independent, and both nest exposure (chick vulnerability to predation) and the risk of adult predation at the colony have

also been identified as potential selective pressures determining the evolution of the different chick developmental strategies in the Alcidae (Birkhead & Harris 1985, Ydenberg 1989, Gaston 1992).

Patterns of parental care within the Alcini are further complicated by differences in diet. The Little Auk is the only planktivorous species of the otherwise piscivorous tribe. Prey availability may be an important factor influencing parental decisions (Fraser *et al.* 2002). Simultaneous study within the Alcini of both parental foraging effort and the spatial and temporal variation in prey availability and energetic value is needed to clarify the role of dietary differences in patterns of parental care.

A fuller understanding of the evolution of the strategy of parental care in the Little Auk will require more detailed studies of sex differences in investment over the breeding season; the influence of parental behaviour on condition, over-winter survival, mate fidelity and breeding success in the following season; the relationship between uniparental care and chick requirements at the end of chick-rearing; the independence of parental care decisions within pairs (McNamara *et al.* 2002); and the plasticity in sex roles.

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